

NODAL ANATOMY IN RETROSPECT

I. W. BAILEY

INTRODUCTION

IN 1913, Professor E. W. Sinnott and I initiated a series of cooperative investigations on the phylogeny of the angiosperms which led us to the publication of nine papers between 1914 and 1918. Summations of evidence accumulated during the last forty years have supported and strengthened our contention (20) that ancestral angiosperms were relatively large woody perennials, and that the herbaceous habit in dicotyledons is a derived, rather than a primitive one. Similarly, much additional information has verified our conclusion (1) that the structure of the xylem in such representatives of the Amentiferae as the Casuarinaceae, Betulaceae and Fagaceae is relatively highly specialized rather than truly primitive. On the contrary, our conclusions regarding the ancestral form and vasculature of the angiospermic leaf need reconsideration in the light of investigations of a wider range of material.

GENERALIZATIONS REGARDING NODAL ANATOMY

As a result of an extensive reconnaissance of 34 orders and 164 families of dicotyledons, Sinnott (18) emphasized the fact that there are three significant forms of foliar nodal anatomy in angiosperms, viz., the *unilacunar* form, in which the vascular supply of the leaf is related to a single gap in the stele, the *trilacunar* form, in which the vascular strands are related to three distinct and more or less widely separated gaps, and the *multilacunar* form, in which numerous lateral vascular strands are related to independent gaps. Although a number of dicotyledonous families are pre-eminently unilacunar, trilacunar or multilacunar — thus providing significant evidence in the identification and classification of plants — there are a considerable number of families and numerous orders in which transitions between the different forms of nodal anatomy occur. Sinnott concluded that the trilacunar condition is primitive in angiosperms, the multilacunar form having arisen by amplification of the number of independently attached lateral strands, and the unilacunar form (a) in certain families, by the reduction and elimination of the two lateral strands and (b) in other families, by the approximation of the median and lateral strands forming an aggregation of three strands that is related to a single gap in the stele.

These conclusions, in which I concurred, were based upon putative phylogenetic evidence derived from the angiosperms as a whole, and upon ontogenetic sequences that occur in the developments of specific plants. The trilacunar condition tends to predominate in a majority of the families of the

Archichlamydeae, the unilacunar structure in the Centrospermae, Myrtiflorae and a majority of the families of the Metachlamydeae. The multilacunar condition is characteristic of many of the Polygonaceae, Platanaceae, Simarubaceae, Burseraceae, Meliaceae, Araliaceae and Umbelliferae. Transitions to unilacunar structures frequently occur in trilacunar families in representatives which exhibit an enhanced degree of both floral and anatomical specialization. Similarly, aberrant transitions to multilacunar nodal anatomy occur in many predominantly trilacunar orders and families. Where the leaves of adult plants are multilacunar, the first-formed leaves of seedlings commonly are trilacunar with transitions to the typical multilacunar condition in successively formed ones. Similarly, the first leaves of monocotyledonous seedlings frequently have three independently attached vascular strands, thus resembling the trilacunar-like structure that occurs in the adult leaves of putatively more primitive representatives of the Potamogetonaceae.

STATISTICAL CORRELATIONS REGARDING LEAF FORM

In a subsequent comprehensive survey of 156 families of dicotyledons, we (19) demonstrated that there is an evident correlation between nodal anatomy and the formation of stipules. Of 75 of these families, which have stipules or leaf sheaths, 53 are characterized by having trilacunar or multilacunar nodal structure, and in five others this form of nodal anatomy is common. In 16 of these stipulate families the nodes are unilacunar, but in 11 of them the stipules frequently are poorly developed, minute or absent. Conversely, of 81 exstipulate families 52 are characteristically unilacunar and two more are frequently so. Where unilacunar structure occurs in aberrant genera or species of dominantly stipulate and trilacunar families, such plants commonly exhibit reduction or elimination of stipules. Conversely, aberrant trilacunar representatives of dominantly unilacunar families not infrequently have well-developed stipules in contrast to their unilacunar relatives. Among exstipulate trilacunar families approximately 75% of the plants have leaves or leaflets with entire margins. Thus, the fullest development of stipules occurs in trilacunar families having lobed leaves or leaves with dentate, serrate or glandular margins, whereas the strongest tendency toward the reduction and elimination of stipules occurs in unilacunar families having leaves with entire margins. It is significant in these connections that the vasculature of most stipules is related to the lateral vascular strands at some level of the node or petiole.

As a result of extensive statistical analyses of dicotyledonous floras in diversified phytogeographical regions of the principal continental areas, we (21) concluded that the primitive angiospermic leaf was simple, palmately veined, probably 3-lobed, and was provided with three main vascular strands which were attached at a trilacunar node. These conclusions were based upon evidence from *paleobotany*, that the palmate leaf was more frequent in the Cretaceous and Tertiary than at present; from *comparative morphology*, (a) that there is a correlation between the palmate leaf and

trilacunar (and multilacunar) nodes, (b) that there is a strong correlation between the simple pinnate leaf and the unilacunar node, (c) that palmate or parallel venation tends to predominate in cotyledons and floral appendages; and from *phylogeny*, that palmate leaves are more frequent in relatively primitive groups of dicotyledons and that pinnate leaves are commoner in more advanced ones. Furthermore, among woody plants the trilacunar (more ancient) nodal condition predominates in temperate regions, and the unilacunar (more advanced) in the tropics. The palmately lobed leaf among woody plants is largely confined to temperate regions. These facts, in company with others, suggested that the dicotyledons first appeared under a climate more temperate than tropical, a climate in the Mesozoic presumably found extensively only in the uplands.

REVIEW OF PHYLOGENETIC EVIDENCE

The most comprehensive and reliable phylogenetic sequence thus far revealed among the higher plants is the derivation of vessels from scalariformly pitted tracheids in the angiosperms. As demonstrated by large volumes of data successively accumulated during the last 40 years, the complete evolutionary story is preserved among living angiosperms, and it is no longer essential to search geological strata for "missing links." Furthermore, this particular phylogenetic sequence clearly is a unidirectional and irreversible one, and cannot be read in reverse, as so frequently happens, since in view of available information regarding the structure of the lower vascular land plants tracheids cannot logically be derived from the dissociated members of vessels.

It should be emphasized in this connection that the evolution and specialization of vessels in angiosperms have been reconstructed *entirely independently* of assumptions regarding the relative 'primitiveness' of specific orders, families or other taxa of the angiosperms. Although primitive vesselless forms of dicotyledonous xylem are confined at present to woody plants of putative ranalian affinities, viz., Winteraceae, *Trochodendron*, *Tetracentron*, *Amborella* and *Sarcandra*, relatively primitive stages in the evolution of vessels are preserved in such families of the Metachlamydeae as the Clethraceae, Ericaceae, Symplocaceae, Styracaceae and Caprifoliaceae, as well as in various families of the Archichlamydeae. Conversely, highly evolved and specialized vessels occur in many representatives of such putatively primitive taxa of the Archichlamydeae as the Amentiferae, Ranales, Rosales, Malvales, etc. Thus, it is now clearly demonstrated that evolutionary modification of the xylem of stems and roots is *not necessarily* closely synchronized with phylogenetic trends in the specialization of the angiospermic flower. Either trend of evolution may be accelerated or retarded in relation to the other. For example, among primitively vesselless genera of the dicotyledons, certain of them, e.g., *Zygogynum*, *Trochodendron*, *Sarcandra*, exhibit advanced stages of floral specialization. Therefore, although one of the various classifications of the angiosperms may possibly provide a fairly accurate picture of certain

aspects of floral evolution, it evidently does not afford a truly phylogenetic classification of the plants which bear the flowers, i.e., when evidence from all organs and parts of the plants is taken into consideration. Nor can a truly natural classification of plants as a whole be attained by substituting phylogenetic trends, however reliable, from another **single** organ or part of the plant.

In view of such facts as these, there obviously are inherent difficulties and dangers in attempting to determine the primitive form and vasculature of the angiospermic leaf by statistical analyses of the various families and orders of the Archichlamydeae as contrasted with the Metachlamydeae, or in basing conclusions upon speculative assumptions that have been made regarding the relative primitiveness of the Amentiferae, Ranales, Rosales, Malvales, etc.

In the case of the vessel, paleobotanical evidence demonstrates that it can be derived only by modification of *one* type of cell, viz., tracheid. On the contrary, in the case of the angiospermic leaf, the possibility exists that it may have been derived from one of *several* diversified forms of potentially ancestral foliar appendages. Furthermore, the possibility exists that changes in form and vasculature may at times be reversible. In other words, in the case of the vessel convincing evidence is now available regarding initial stages of a unidirectional and irreversible evolutionary trend, whereas in the case of the leaf no comparably reliable information is available as yet.

REVIEW OF NODAL ANATOMY

Sinnott's and my conclusions regarding the primitive form of the angiospermic leaf were based largely upon our contention that in angiosperms unilacunar and multilacunar nodal structures are derived from a primitive trilacunar one. Since a similar working hypothesis was subsequently adopted by Eames (6) in the study of floral appendages, it is evident that nodal anatomy became the keystone in a large volume of phylogenetic investigation. Thus, it is essential to determine how reliable a working hypothesis is provided by nodal anatomy.

Among ferns, seed ferns, Cordaitales, Bennettitales (*sensu lato*), Coniferales, *Ginkgo* and *Ephedra*, the vascular strands of the leaf, whether one, two or many, are related to a single gap in the primary body. Deviations from this prevailing *unilacunar* condition occur, however, in the living cycads and in *Gnetum*, where numerous foliar strands are related to an equivalent number of independent gaps in the stele. Such evidence from the lower Pteropsida suggests that a unilacunar type of node is primitive, and that the multilacunar condition among gymnosperms is a derived and specialized one. Therefore, the trilacunar and multilacunar structures of angiosperms must have been derived at some evolutionary stage from a unilacunar condition. Whether the transition occurred within the angiosperms themselves or during the evolution of their ancestors is a basic problem in need of solution. Are all forms of unilacunar nodes homologous or are there

fundamental structural differences that have been overlooked? If the early angiosperms acquired a pair of independently attached foliar strands and subsequently eliminated them by reduction or approximation, does the resulting unilacunar condition differ structurally from the primitive nodal anatomy of the lower Pteropsida?

Much of the work in the past has dealt with comparative investigations of fully matured structures at nodal levels. Such comparative studies of end products have proven to be of significant value in the identification and classification of plants, but, without comprehensive developmental investigations at successive levels of the shoot and leaf, they may be misleading at times in the study of phylogeny.

There has been an increasing tendency of late to visualize the vasculature of the stem and its appendages in terms of the "Telome Theory." Thus, particularly in the case of the Cordaitales and Coniferales, the leaf trace is illustrated as a single strand which may dichotomize one or more times in its upward extension into the leaf. In such plants there may be two separate vascular strands (related to a single gap) at the nodal level, with more or less numerous additional dichotomies occurring within the lamina of the leaf. It is significant in this connection, however, that in *Ginkgo biloba* L. as demonstrated by Gunckel and Wetmore (11, 12), in certain species of *Ephedra* (14, 15), and in such dicotyledons as *Austrobaileya* (3, 14), *Trimenia* (14, 16), *Ascarina* (22), *Lactoris* (23), and *Clerodendron trichotomum* Thunb. (14), although there are two separate vascular strands related to a single gap at the nodal level, these strands do not unite at lower levels but retain their individuality and are connected to *two entirely independent bundle systems of the eustele*. This raises the question whether there are two fundamentally different types of vasculature within the Pteropsida or merely extreme deviations from a single basic type.

In *Ginkgo*, the vasculature of the lamina is typically dichotomous, the veins of the two bilateral halves of the leaf being related, however, to two independent parts of the eustele. Therefore, the number of veins tends to be a multiple of two, viz., an *even* number. This is in marked contrast to the vasculature of many dicotyledonous leaves which tend to have an *odd* number of vascular strands at the nodal level. How does a transition from an *even* to an *odd* number of vascular strands occur?

In those representatives of the Coniferales which have a single vascular strand in the leaf and at nodal levels, the vasculature might be due to a suppression of dichotomies correlated with extreme reduction in the breadth of the lamina of the leaf. On the contrary, in dicotyledons which have relatively broad leaves and a single vascular strand at the nodal level, the strand frequently is resolved at subnodal levels into two independent traces. In other words, the single strand at the nodal level may be interpreted as having evolved by *fusion* of *two* independent traces rather than by suppression of the dichotomy of a *single* trace.

In this connection, recent investigations of the Chloranthaceae, Lactoridaceae, Amborellaceae, Trimeniaceae, Austrobaileyaceae, Monimiaceae,

Lauraceae, Gomortegaceae and Hernandiaceae have revealed considerable significant evidence. The *totality* of morphological characters from different organs and parts indicates that these families are relatively closely related and constitute one of two major categories of the woody Ranales (*sensu lato*). With a few exceptions, which will be discussed subsequently, all of the numerous genera have prevailing unilacunar nodes and simple leaves with characteristically pinnate venation. The xylem of the various genera exhibits numerous successive evolutionary stages in the development of vessels; that of *Sarcandra* (24) and *Amborella* (2) being of a primitive vesselless form, whereas that of the Hernandiaceae contains vessels of a highly evolved and specialized structure.

In *Ascarina* (22), *Austrobaileya* (3), *Lactoris* (23) and *Trimenia* (16), there are two independent foliar traces which extend upward to the nodal level and into the petiole of the leaf. These vascular strands may remain distinct and separate throughout the costa of the lamina or they may fuse to form a single mid-vein, particularly in the middle and upper parts of the lamina. Thus, each bilateral half of the simple, pinnately veined leaf is vascularized by minor lateral ramifications of an independent foliar trace. In *Amborella* (2) and in certain representatives of the Monimiaceae (16) fusion of the two principal strands to form a single broad arc of vascular tissue extends downward to the nodal level, giving the impression, *except at lower levels*, that the leaf is vascularized by a single foliar trace.

In *Piptocalyx* (16), a close relative of *Trimenia*, the two independent traces tend to dichotomize, forming four strands in their upward course toward the base of the leaf. The two central strands commonly fuse at the nodal level or in the basal part of the petiole, thus exhibiting a transition from an *even* number (four) to an *odd* number (three) of foliar vascular strands. Numerous representatives of the Monimiaceae likewise have an odd number (three, five, seven, nine) of strands at the nodal level. That these strands commonly result from the bifurcation of two independent traces may be demonstrated by tracing them downward through two internodes of the stem. In many cases at least, the odd number of strands at the nodal level is due to the fusion of strands that belong to two independent systems of vasculature. Such a pattern of dichotomy and fusion occurs in many species of *Hedyosmum* (22), where there are usually five strands at the nodal level and in the base of the petiole.

In all of the numerous genera of these families, with the possible exception of *Sarcandra* and *Chloranthus*, there is no evidence which may be interpreted as indicative of the derivation of a unilacunar from a trilacunar form of nodal structure. The occurrence of three strands (as well as one, two, four, five, six, seven or nine) at the nodal level cannot be accepted as unquestionable evidence of a transition to unilacunar vasculature by the approximation of three separate strands of a trilacunar node.

Within the Chloranthaceae (22) *Ascarina*, as previously noted, has two independent traces which pass upward to the nodal level and extend out-

ward through the petiole into the lamina of the leaf. In *Hedyosmum* the two traces divide in their upward course, forming six strands, the two slender central members of which tend to unite at the nodal level. Thus, at this level, the leaf appears to be vascularized by an odd number (five) of primary strands. *Sarcandra* and *Chloranthus* resemble *Ascarina* in having two massive independent traces which extend upward into the leaf. Most of the bilateral vasculature of the pinnately veined lamina is related to these two conspicuous strands. However, the basic pattern of vasculature is complicated in the petiole and at the nodal level by the occurrence of three small additional strands. The medianly located one of these is formed, as in *Hedyosmum*, by the fusion of minor branches of the two subtending leaf traces. The other minor strands are laterally situated and are related to independent traces at separate gaps in the eustele. In most dicotyledons having opposite leaves and trilacunar structure, there are six gaps at the nodal level, i.e., three independent gaps for each leaf, compare *Fig. 1, G*. In *Sarcandra* and *Chloranthus* there are four gaps, two median ones facing the leaves as in *Ascarina* and *Hedyosmum* and two lateral ones in addition. The corresponding lateral strands of the two leaves fuse at the nodal level and are jointly related to these gaps, compare *Fig. 1, F*. However, at lower levels they separate and become attached to independent parts of the eustele. *A priori* there is no convincing evidence for interpreting this aberrant form of vasculature as a transition from trilacunar to unilacunar nodal structure rather than *vice versa*. Indeed, the totality of evidence indicates that there is a fundamental *double* system of vasculature throughout all representatives of this group of families; transitions from an even to an odd number of vascular strands occurring at different levels. Furthermore, it suggests that pairs of independently attached lateral strands may be added without necessarily modifying the number of principal strands that are related to the median gap in the eustele.

There are other categories of dicotyledons where a summation of evidence is indicative of a transition from unilacunar to trilacunar or multilacunar nodal anatomy rather than *vice versa*. For example, a majority of the Ericales are characterized by having simple pinnately veined leaves and unilacunar nodes. However, there is an aberrant tendency in the Epacridaceae, as in the Thibaudieae of the Ericaceae, to form leaves with palmately parallel venation. As emphasized by Dormer (5), only five of the more than twenty genera of the Epacridaceae have leaves with sheathing bases. Two of these, *Richea* and *Dracophyllum*, differ markedly from the rest of the Epacridaceae, and from other representatives of the Ericales, in having trilacunar and multilacunar nodes. Thus, in the case of the Epacridaceae, as of the Chloranthaceae, a *totality* of evidence is indicative of the derivation of trilacunar and multilacunar nodes from a unilacunar one. This is in marked contrast to conditions in such families as the Leguminosae, Anacardiaceae, etc., where certain genera or species exhibit reduction from trilacunar to unilacunar nodes.

A summation of evidence from the dicotyledons as a whole indicates,

therefore, that conspicuous modifications of nodal structure are reversible, pairs of independently attached lateral strands being added in certain cases and eliminated in others. Furthermore, the addition or subtraction of pairs of independently attached strands can occur without fundamental changes in the number of the vascular strands related to the median gap of the node. Thus, more emphasis should be placed in the future upon studying vascular tissues related to the median gap and upon tracing their extensions downward into lower levels of the stem. Transitions from an *even* to an *odd* number of traces appear to be of considerable significance in the phylogeny of the Pteropsida and in discussions of "Telomic" interpretations of vascularization patterns.

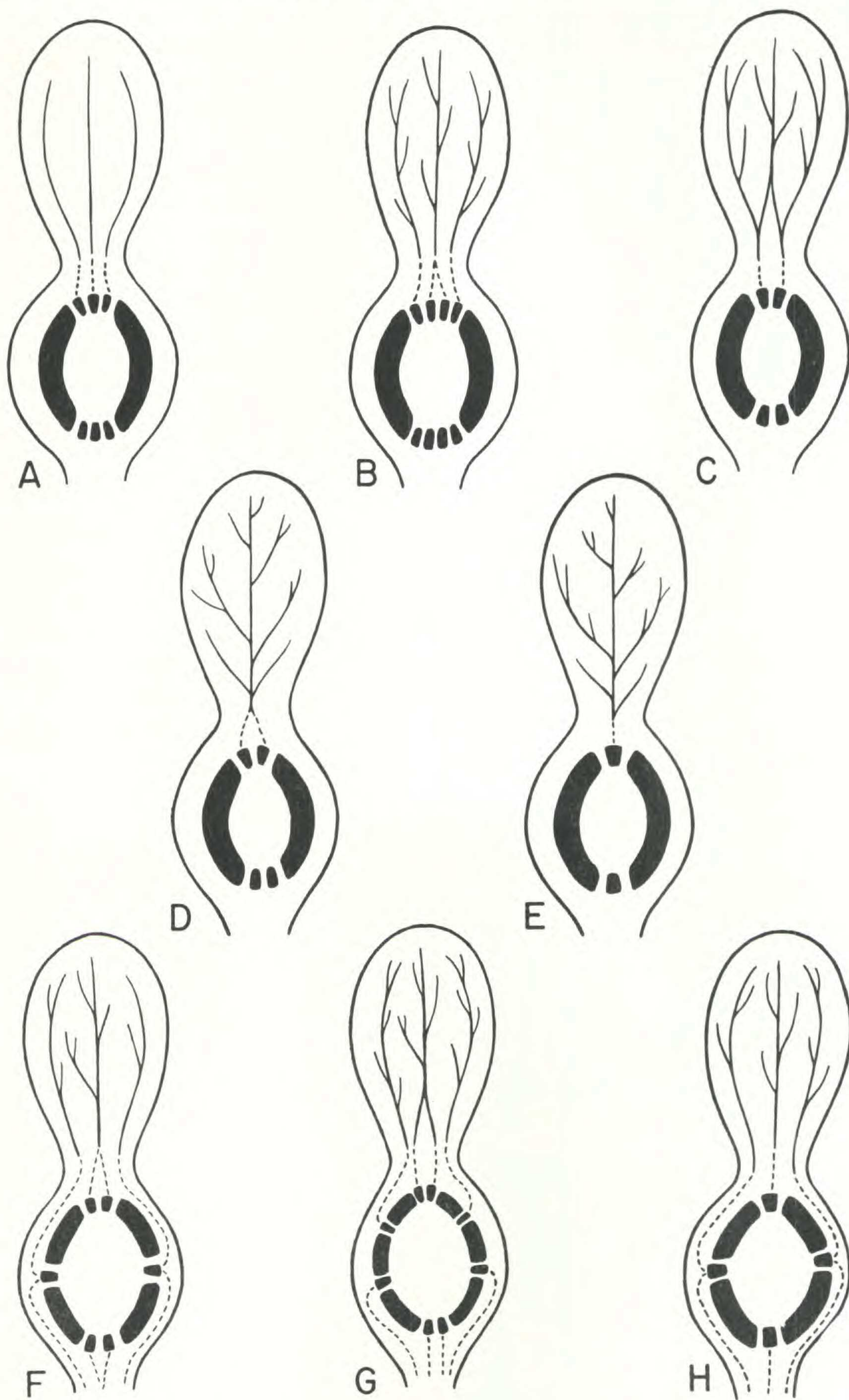
DEVELOPMENTAL INVESTIGATIONS

At present there is a dearth of reliable information regarding the extensions of leaf traces below the nodal level. Successive stages in the development of procambium, phloem, and xylem have been investigated by adequate modern techniques in a very limited number of genera and species. However, Nägeli's (17) numerous illustrations, coupled with the detailed investigation of *Linum* by Esau (7, 8) and Girolami (10), of *Sambucus* and *Helianthus* by Esau (9), and my own preliminary studies of a considerable number of dicotyledons, indicate that the leaf trace related to the median gap of the node (when followed downward) frequently forks above the next subtending leaf of an orthostichy. In other words, the halves of the leaf trace are related at lower levels to two independent parts of the eustele. This suggests (from ontogenetic and phylogenetic points of view) a fusion of two independent strands, and does not support telomic illustrations of a single trace which dichotomizes in its upward extension. Furthermore, the lateral traces of trilacunar and multilacunar nodes do not unite in most cases to form a single strand at lower levels.

NODAL ANATOMY AND VASCULATURE OF SEEDLINGS

As demonstrated in Lubbock's (13) comprehensive treatment of dicotyledonous seedlings, a majority of their cotyledons are simple and entire. However, there is a wide range of variability in form from broadly elliptical, orbicular, ovate, obovate, cordate or reniform to oblanceolate, spatulate or linear, and from sessile to extensively petiolate. Although palmately lobed, trifid, tripartite or multifid cotyledons are comparatively rare, emarginate, bilobed, bifid and auriculate forms are of not infrequent occurrence in various families.

As emphasized by Lubbock and others, there is a striking difference in form between the cotyledons and leaves of specific seedlings. This is particularly conspicuous in families having serrate, dentate, lobed, cleft, divided or compound leaves. Instances, e.g., Onagraceae, where the cotyledons assume a form during the later stages of their enlargement which



TEXT-FIG. 1. A-H, forms of cotyledonary nodal anatomy in dicotyledons.

closely resembles that of the first-formed leaves, are of exceptional rather than of common occurrence. In other words, although there is a similar range of variability in the form of cotyledons as among leaves, similar forms of cotyledons and leaves rarely occur in close association on the same seedling.

A reconnaissance of seedlings obtained from 99 families of the dicotyledons reveals a range of variability in cotyledonary nodal anatomy that is illustrated in *Fig. 1*. These patterns resemble structures that are known to occur at foliar nodes having opposite leaves. It is significant in this connection, however, that cotyledons with multilacunar attachments are rare, and that the frequency of occurrence of the unilacunar and trilacunar forms differs considerably in the case of cotyledons as contrasted with leaves.

Among cotyledons of the species investigated, 77% have an *even* number of vascular strands at the nodal level (*B*, *C*, *D*, *F* & *G*), and 60% of them have *two* independent traces that are related to a single gap (*C* & *D*). The latter double-trace, unilacunar form of nodal structure is not confined to a few specific genera, but evidently is of common occurrence in many orders and families of the dicotyledons. This is in marked contrast to foliar nodes where a large majority of dicotyledonous leaves are reported to have an *odd* number of traces and where the double-trace unilacunar form of structure has been encountered thus far in a limited number of families, viz., certain representatives of the Austrobaileyaceae, Trimeniaceae, Chloranthaceae, Lactoridaceae, Verbenaceae, Labiatae and Solanaceae.

Of the cotyledonary nodal patterns illustrated in *Fig. 1*, (*B*), present in 7% of the seedlings investigated, and forms (*F*) and (*G*), in 10% of them, are apparently of infrequent occurrence at foliar nodes. Form (*B*) has, however, been encountered at certain of the foliar nodes of *Piptocalyx* and form (*F*) at those of *Sargentodoxa*. On the contrary, form (*A*), having *three* strands related to a single gap, is of less frequent occurrence at cotyledonary nodes although commonly encountered at foliar ones.

In the case of leaves arranged in an opposite or decussate phyllotaxy and having one pair of independently attached lateral vascular strands, there usually are, as previously stated, six gaps at the nodal level, viz., three related to each of two leaves. Although this type of structure occurs at times at cotyledonary nodes (*G*), it is much less common than the arrangement illustrated in patterns (*F*) and (*H*) where the corresponding laterals of the two cotyledons unite and are related to two, instead of to four, independent lateral gaps. Although uncommon, this modification of trilacunar structure occurs as previously stated at the foliar nodes of *Chloranthus* and *Sarcandra*, and has been encountered at those of certain representatives of other families, e.g., Rubiaceae.

Thus, a reconnaissance of seedlings indicates that there is a range of structural variability in cotyledonary nodes similar to that found in foliar ones. The fundamental differences between the vasculature of leaves and cotyledons at the nodal level are quantitative rather than qualitative, an

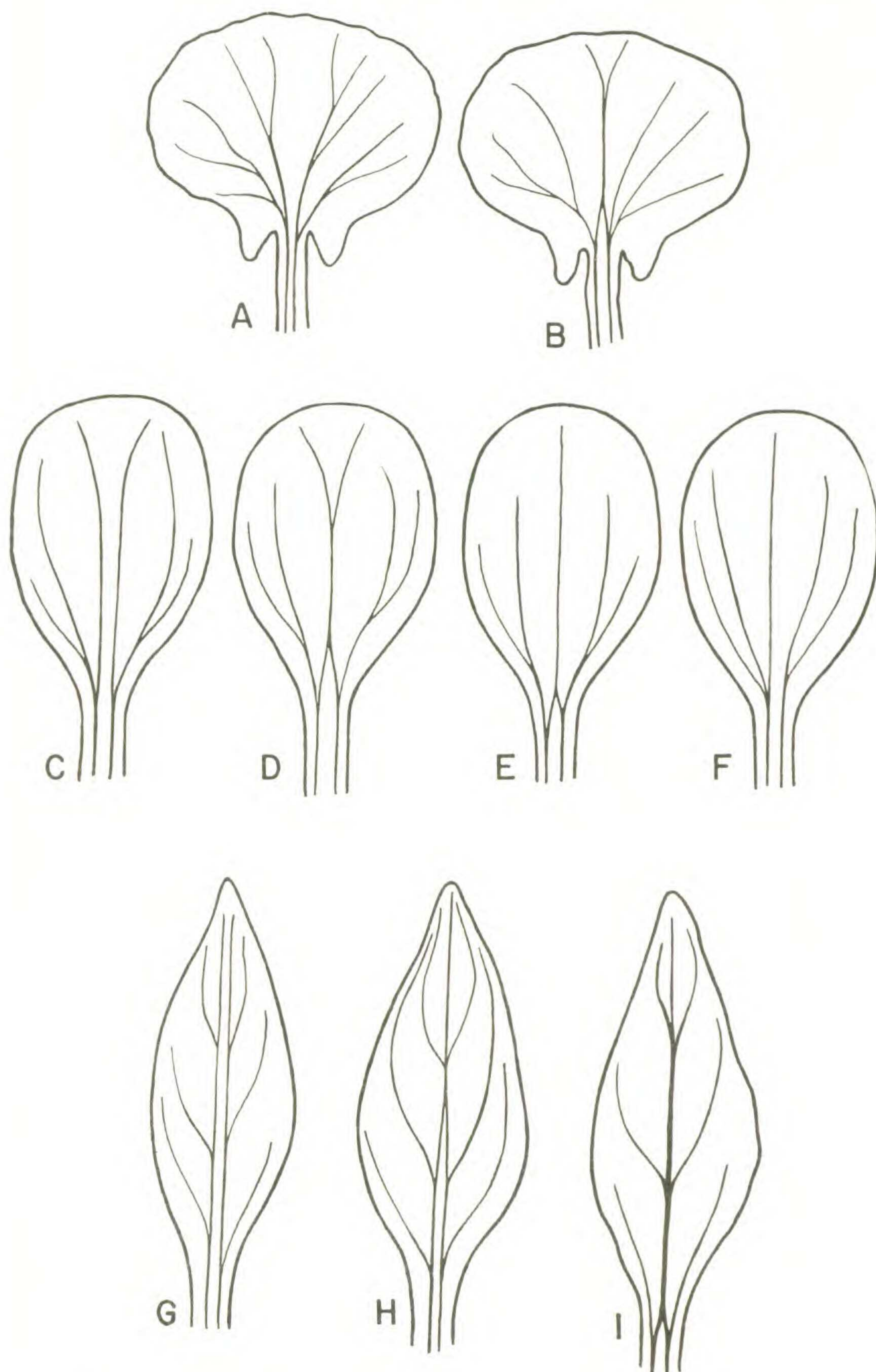
even number of vascular strands being commoner in the case of cotyledons and an *odd* number in the case of leaves

It should be noted in this connection, however, that cotyledons with multilacunar attachments do not occur in any of the seedlings that I have studied, even in families where the leaves of adult plants are attached at multilacunar nodes. Although cotyledons with pentalacunar vasculatures have been demonstrated by Carlquist (4) to occur in *Fitchia speciosa* Cheeseman, there are reasons for believing that multilacunar attachments will prove to be of infrequent occurrence in the dicotyledons as a whole. In families having multilacunar foliar nodes, e.g., Magnoliaceae, Polygonaceae, Umbelliferae, etc., the leaves are arranged prevailingly in alternate rather than in opposite phyllotaxy. There appear to be spatial and other difficulties in the development of multilacunar nodes where the leaves are opposite. Furthermore, as previously noted, where the leaves of adult plants are multilacunar the first leaf of the seedling commonly tends to be trilacunar with transitions to the typical adult multilacunar condition occurring in subsequently formed leaves of the young plant. The cotyledonary nodes of such plants are either of the unilacunar type (viz., having two gaps, one for each of the opposite cotyledons) or of the trilacunar forms illustrated in (F), (G) and (H). In this respect, the seedlings of such plants with multilacunar foliar nodes resemble those of the multilacunar living cycads and *Gnetum*.

It should be emphasized in this connection that, if the trilacunar condition is primitive in angiosperms, and if the ontogenetic sequences in the preceding paragraph are to be interpreted as recapitulations of the phylogenetic derivation of multilacunar nodes from trilacunar ones, then one might anticipate finding ontogenetic sequences in seedlings illustrating the reduction of trilacunar nodes to unilacunar ones. Although a considerable number of seedlings that I have examined have a first-formed leaf attached at a unilacunar node in contrast to the trilacunar or even the multilacunar nodes of the adult plant, I have not succeeded thus far in finding a succession of seedling leaves which exhibit an ontogenetic transition from trilacunar to unilacunar structure.

As previously emphasized by Sinnott and myself (21), many cotyledons are characterized by having a pseudo-palmate or palmate-parallel venation. In such cotyledons, there commonly are three or five conspicuous primary veins that extend outward from a locus at the base of the cotyledon, the lateral ones diverging and extending parallel to the margins of the lamina, *Fig. 1, C, Fig. 2, E*. A large number of these cotyledons show a transition from an *even* number (two) of vascular strands at the nodal level to an *odd* number (three or five) of primary veins in the lamina. The outward extensions of the two independent traces commonly divide in the petiole or the base of the lamina, forming four or six strands, the two central members of which unite to form a mid-vein, *Fig. 2, E*.

There are numerous deviations and aberrations of this common form of pseudo-palmate vasculature, not only among different families and genera, but also among seedlings of the same genus or species. The branches of



TEXT-FIG. 2. A-I, forms of cotyledonary venation in dicotyledons.

the two traces may remain independent throughout the lamina, *Fig. 2, A & C*, or the two central ones may approximate and then diverge toward the apex of the cotyledon, *Fig. 2, D*. Where the branching is symmetrical, *Fig. 2, A & C*, there is an *even* number of conspicuous veins in the lamina. On the contrary, where the branching is asymmetrical, as sometimes happens, *Fig. 2, F*, a single branch of one trace may assume the position of a mid-vein, and there may be an *odd* number of conspicuous veins in the lamina.

The phenomena of dichotomy and fusion, which lead to a transition from an even to an odd number of vascular strands, may occur at different levels of the lamina, the petiole or the nodal and subnodal regions. Where the dichotomy is precocious, there may be four or even six strands related to a single gap at the nodal level, *Fig. 1, B*. Conversely, where the concrescence of independent strands is precocious, there may be a single strand at the node, *Fig. 1, E*, or in the petiole, *Fig. 1, D*, with one, three or five conspicuous veins diverging from it in the base of the lamina. Where both dichotomy and concrescence are precocious, there may be three strands related to a single gap at the nodal level, *Fig. 1, A*. In the case of cotyledons having more than two strands at the level of attachment, two or more of the basal lateral veins of the lamina commonly are in direct continuity with independent traces, related either to a single gap, *Fig. 1, A & B*, or to independent lateral gaps, *F, G, & H*.

It should be noted in this connection that there are numerous cotyledons which exhibit intermediate or transitional forms of vasculature between these pseudo-palmate patterns and typically pinnate ones. In such cotyledons, the basal lateral veins are less conspicuous and extensive and the apical branches of the mid-vein are correspondingly emphasized, *Fig. 2, H & I*. It is significant, however, that even the narrower forms of pinnately veined cotyledons commonly exhibit a vasculature that is related at some level to two independent vascular strands or traces. As in the pinnately veined leaves of *Austrobaileya*, *Trimenia* and *Ascarina*, two traces may extend independently throughout a cotyledon, *Fig. 2, G*, or they may become concrescent at varying levels of the lamina, *Fig. 2, H*, of the petiole, *Fig. 2, I*, or of the node, *Fig. 1, E*.

There appears to be no conspicuous and universal correlation between the form and venation of cotyledons and specific types of nodal structure. Cotyledons of widely varying form and venation may have a similar basal vasculature. Conversely, cotyledons of similar form may be attached at strikingly different nodes. However, there does appear to be a higher percentage of pinnate venation among cotyledons which are attached at single-trace unilacunar nodes.

Occasionally there is a considerable range of variability in the vasculature of cotyledons grown from the seed of a single plant, and at times in the two cotyledons of a single seedling. For example, one cotyledon may have four vascular strands related to a single gap at the nodal level, *Fig. 1, B*, whereas the opposite cotyledon has one or two of these strands attached at independent gaps, *Fig. 1, G*. The branches of two traces

may extend independently throughout the lamina of one cotyledon, *Fig. 2, A, C, F & G*, whereas approximation and concrescence of branches to form a mid-vein occur in another cotyledon, *Fig. 2, B, E, H & I*.

VASCULATURE OF FLORAL APPENDAGES

The nodal anatomy of floral bracts, bracteoles, and the independent parts of polysepalous calyces frequently resembles that of the leaves of the plant upon which the flowers are borne. However, there are numerous deviations, and the venation of free sepals, as of petals, tends in many cases to be pseudo-palmate even where the leaves have a typical pinnate venation. The folded megasporophylls of apocarpous flowers also tend to have a palmate-parallel venation, the basal vasculature varying from unilacunar to trilacunar to multilacunar. According to Eames (6), the 3-veined (one dorsal and two ventrals) trilacunar form of carpel is primitive, the unilacunar and multilacunar forms having developed from it by obvious trends of simplification and amplification. Most stamens have a single vascular strand that is related to a unilacunar node.

Recent investigations of a number of the less well known tropical and subtropical representatives of the woody Ranales (*sensu lato*) have revealed evidences of what appear to be primitive forms of floral morphology. Among such plants there are various stages in the differentiation of sterile appendages into bracteoles, sepals and petals. There are broad microsporophylls which are not differentiated into filament, anther and connective, and unsealed, styleless megasporophylls with widely diffused stigmatic surfaces.

The carpels of the less specialized flowers of the Winteraceae resemble conduplicately folded, emarginate, pseudo-palmate, 3-veined cotyledons. The microsporophylls and staminodes of *Degeneria* and *Himantandra* also have a palmate-parallel, 3-veined vasculature, as do many of the stamens of the Magnoliaceae. Such occurrences strengthen Eames's contention that primitive carpels and stamens were conspicuously 3-veined sporophylls. In the case of carpels, the elimination of a stipe, incipient adnation to the torus, sterilization of the upper part of the megasporophyll as a concomitant of the formation of a style, reduction in the number of ovules, and diverse forms of adnation and cohesion tend more or less extensively to modify this primitive vasculature. In the case of the stamen, reduction in the lamina of the microsporophyll, increasing protuberance of the sporangia, and the formation of a comparatively slender filament appear to have resulted in the suppression and elimination of the lateral veins, leaving a single median vascular strand.

Although the venation of relatively primitive forms of carpels and stamens tends to be comparatively stable within a flower, their vasculature at nodal and subnodal levels commonly is variable even in a single specimen, as might be anticipated from a developmental point of view where numerous appendages are congested upon the broadened apex of a pedicel. The three principal veins of one carpel or stamen may be

related to a single trace (unilacunar) at the nodal level, those of another may be related to three approximated traces (unilacunar), whereas those of a third are related to three widely separated traces (trilacunar).

Transitions from an even (two or four) to an odd (one or three) number of vascular strands are apparently of infrequent occurrence even in the subnodal levels of floral axes. However, in *Austrobaileya* (3) the dorsal vein of the carpels, the mid-vein of the broad microsporophylls, and the veins of the staminodia, tepals and bracteoles are related at lower levels to two separate traces which are related in turn to two separate parts of the eustele. Furthermore, in the case of *Sarcandra* (24), a vesselless representative of the Chloranthaceae, there is a single stamen that is basally adnate to a carpel. The mid-vein of the stamen usually is double. Not only may the paired veins run independently throughout the stamen, but also they are related at lower levels to two independent bundles of the eustele. Transitions from *two* independent strands to *one* occur at times and at different levels by concrescence of the two strands. The carpel of *S. glaber* has a double dorsal vein and two ventrals which may be widely separated or closely approximated. The carpel of *S. hainanensis*, on the contrary, not only has a single dorsal vein, but also a single ventral one due presumably to the concrescence of two ventral veins or to the suppression of one of them.

Although detailed developmental investigations are likely to reveal additional instances of doubleness in the subtending traces of floral appendages, it is unlikely that transitions from an even number of traces to an odd number of principal veins will prove to be of as frequent occurrence in the case of stamens and carpels as in the case of leaves and particularly of cotyledons.

It should be noted in these connections that cotyledons and floral appendages are of comparatively limited size, and rarely, if ever, have stipules or a truly compound lamina. Furthermore, where they have the homologue of a petiole, the vasculature does not attain the extreme complexities that occur in the petiole and costa of many leaves. With the exclusion of compound leaves and excessive petiolar complexities, one finds a similar range of potentialities of form and vasculature in cotyledons and floral appendages as in simple leaves with pinnate or palmate venation. The differences between various categories of appendages are quantitative rather than qualitative. Two-trace unilacunar nodes and transitions from an even to an odd number of vascular strands are apparently of decreasing frequency in passing from cotyledons to leaves to stamens and carpels.

DISCUSSION

The data recorded on preceding pages indicate that it is no longer possible to assume that unilacunar nodes in dicotyledons are derived *in all cases* by reduction from a trilacunar condition. Although reduction of trilacunar nodes to unilacunar ones in dicotyledons may ultimately prove

to be of more common occurrence than the reverse phenomenon of amplification from unilacunar to trilacunar, this can be determined with certainty only by more comprehensive and laborious investigations of individual families and orders.

A summation of extensive evidence from the Ranales (*sensu lato*) suggests that during early stages of the evolution and diversification of the dicotyledons, or of their ancestors, certain of the plants developed trilacunar nodes, whereas others retained the primitive unilacunar structure that occurs so characteristically in ferns, seed ferns, Bennettitales (*sensu lato*), Cordaitales, Coniferales, *Ginkgo* and *Ephedra*. Furthermore, a broad survey of seedlings of both dicotyledons and monocotyledons — as well as of those of the living cycads and *Gnetum* — indicates that, where adult plants have developed trilacunar and multilacunar nodes, the cotyledons and first juvenile leaves commonly exhibit a retardation or inhibition of the tendency to form one or more pairs of independently attached lateral traces.

In addition, a summation of seedling evidence accentuates the significance of the occurrence of two independent systems of foliar vasculature in such dicotyledonous families as the Austrobaileyaceae, Trimeniaceae, Chloranthaceae and Lactoridaceae. It necessitates a re-evaluation of the "Theory of the double leaf trace" briefly outlined in 1907 by Thomas (25).

It should be emphasized in this connection that the double-trace unilacunar form of vasculature of leaves, *as of buds*, is significant from physiological, as well as from morphological points of view. An actively transpiring appendage with this form of attachment is able to tap more conducting tissue of the primary body of the main axis than it would be able to do if connected to a single vascular strand at lower levels of the eustele. Transitions from unilacunar to trilacunar and multilacunar structures not only insure more numerous contacts with the conducting strands of the eustele of the stem, but also can provide mechanically stronger attachments at the nodal level.

It is of interest, accordingly, to inquire whether a double-trace pattern of vasculature is a primitive basic form in Pteropsida from which others have been derived by various trends of structural modification. Does a single-trace unilacunar structure arise in all cases by the approximation and fusion of two originally independent vascular strands? Data obtained from nodes and leaves of adult shoots, without reliable information regarding the development and attachment of leaf traces in subnodal parts of the stem, are inadequate for fully answering the question. Although the vascular tissues related to unilacunar nodes, and to the median gap of trilacunar ones, have been demonstrated in an increasing number of cases to be related at lower levels of an orthostichy to two independent parts of the eustele, it is not known at present whether such attachments predominate in the dicotyledons and in various categories of the gymnosperms. Nor is there reliable evidence to indicate how extreme reductions in the size of leaves, and various xerophytic adaptations, may modify patterns of vasculature. However, reductions of trilacunar to unilacunar nodes

appear in certain dicotyledonous families to be correlated with such modifying factors. Accurate developmental investigations of the Coniferales may prove to be particularly significant in studying the effects of xerophytic tendencies.

It should be noted in passing that the vascular tissues of the primary body are described in terms of steles, bundles, traces and veins. However, in growing shoots of dicotyledons, the leaf traces are composed of long files of vertically contiguous tracheary cells. The individual files may be in contact laterally or they may be separated by parenchymatous elements. During the earlier stages of growth (after the acropetal development of the procambium) they differentiate successively from loci in the base of the leaf, and eventually extend from the lamina of the leaf downward through a varying number of internodes of the stem. From the point of view of translocation, they provide convenient precursors in the development of vessels. Furthermore, even when aggregated in a single trace, they provide independent channels of rapid movement into each bilateral half of a leaf. Thus, traces and veins may be regarded as aggregations of independent channels of rapid translocation, rather than as the most significant units in a system of conduction.

As previously stated, Sinnott and I (21) concluded that the primitive angiospermic leaf was simple, palmately veined, probably 3-lobed, and was provided with three main veins which were attached at a trilacunar node. The occurrence in certain dicotyledonous families of transitions from unilacunar to trilacunar structures and from pinnate to palmate-parallel venation indicates that the evolution of leaf form and vasculature is not a strictly unidirectional and irreversible phenomenon as in the case of the phylogeny of the angiospermic vessel. Furthermore, although relatively primitive forms of carpels and stamens have three conspicuous primary veins, evidence from cotyledons and from the leaves of a number of ranalian and other families raises the possibility that the mid-vein of angiospermic appendages may have evolved by the approximation and fusion of branches of two independent systems of vasculature. However, it should be freely admitted in conclusion that critical paleobotanical evidence is not available as yet for solving the problem of the ancestry of the angiosperms or of the primitive form and vasculature of their appendages.

ACKNOWLEDGMENTS

I am much indebted to Mrs. Margery Marsden Ray for making the illustrations used in this paper. I am also grateful to my colleagues Elso S. Barghoorn, Richard A. Howard, Taylor A. Steeves and Ralph H. Wetmore for their kindness in reading the manuscript and in offering various helpful suggestions.

HARVARD UNIVERSITY HERBARIUM
CAMBRIDGE, MASS.

LITERATURE CITED

1. BAILEY, I. W. and E. W. SINNOTT. Investigations on the phylogeny of the angiosperms. II. Anatomical evidences of reduction in certain of the Amentiferae. Bot. Gaz. **58**: 36-60. 1914.
2. ——— & B. G. L. SWAMY. Amborella trichopoda Baill. A new morphological type of vesselless dicotyledon. Jour. Arnold Arb. **29**: 245-254. 1948.
3. ——— & ———. The morphology and relationships of Austrobaileya. Jour. Arnold Arb. **30**: 211-226. 1949.
4. CARLQUIST, S. J. Personal communication.
5. DORMER, K. J. Morphology of the vegetative shoot in Epacridaceae. New Phytol. **44**: 149-151. 1945.
6. EAMES, A. J. The vascular anatomy of the flower with refutation of carpel polymorphism. Amer. Jour. Bot. **18**: 147-188. 1931.
7. ESAU, K. Vascular differentiation in the vegetative shoot of Linum. I. The procambium. Amer. Jour. Bot. **29**: 738-747. 1942.
8. ———. Vascular differentiation in the vegetative shoot of Linum. II. The first phloem and xylem. Amer. Jour. Bot. **30**: 248-255. 1943.
9. ———. Vascularization of the vegetative shoots of Helianthus and Sambucus. Amer. Jour. Bot. **32**: 18-29. 1945.
10. GIROLAMI, G. Relation between phyllotaxis and primary vascular organization in Linum. Amer. Jour. Bot. **40**: 618-625. 1953.
11. GUNCKEL, J. E. and R. H. WETMORE. Studies on the development of long and short shoots of Ginkgo biloba L. I. The origin and pattern of development of the cortex, pith and procambium. Amer. Jour. Bot. **33**: 285-295. 1946.
12. ——— & ———. Studies on the development of long and short shoots of Ginkgo biloba L. II. Phyllotaxis and organization of the primary vascular system, primary phloem and primary xylem. Amer. Jour. Bot. **33**: 532-543. 1946.
13. LUBBOCK, J. Contribution to our knowledge of seedlings. Appleton and Co., New York. 1892.
14. MARSDEN, M. P. F. and I. W. BAILEY. A fourth type of nodal anatomy in dicotyledons, illustrated by Clerodendron trichotomum Thunb. Jour. Arnold Arb. **36**: 1-51. 1955.
15. ——— & T. A. STEEVES. On the primary vascular system and the nodal anatomy of Ephedra. Jour. Arnold Arb. **36**: 241-258. 1955.
16. MONEY, L. L., I. W. BAILEY and B. G. L. SWAMY. The morphology and relationships of the Monimiaceae. Jour. Arnold Arb. **31**: 372-404. 1950.
17. NÄGELI, C. Das Wachsthum der Stammes und der Wurzel bei den Gefässpflanzen und die Anordnung der Gefässsstränge in Stengel. Beitr. Wiss. Bot. **1**: 1-156. 1858.
18. SINNOTT, E. W. Investigations on the phylogeny of the angiosperms. I. The anatomy of the node as an aid in the classification of angiosperms. Amer. Jour. Bot. **1**: 303-322. 1914.
19. ——— & I. W. BAILEY. Investigation on the phylogeny of the angiosperms. III. Nodal anatomy and the morphology of stipules. Amer. Jour. Bot. **1**: 441-453. 1914.
20. ——— & ———. Investigation on the phylogeny of the angiosperms. IV. The origin and dispersal of herbaceous angiosperms. Ann. Bot. **28**: 547-600. 1914.

21. ——— & ———. Investigation of the phylogeny of the angiosperms. V. Foliar evidence as to the ancestry and early climatic environment of the angiosperms. *Amer. Jour. Bot.* **2**: 1-22. 1915.
22. SWAMY, B. G. L. The morphology and relationships of the Chloranthaceae. *Jour. Arnold Arb.* **34**: 375-408. 1953.
23. ———. Personal communication.
24. ——— & I. W. BAILEY. *Sarcandra*, a vesselless genus of the Chloranthaceae. *Jour. Arnold Arb.* **31**: 117-129. 1950.
25. THOMAS, E. N. A theory of the double leaf trace founded on seedling structure. *New Phytol.* **6**: 77-91. 1907.